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Notes on the Hercules Beetle, *Dynastes hercules* (Linn.), at Rancho Grande, Venezuela, with Special Reference to Combat Behavior.¹

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(Plates I-IV).

[This is one of a series of papers resulting from the 45th and 46th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945 and 1946 under the direction of Dr. William Beebe with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.]

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane cloud forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh water lake of Valencia, and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C; the average annual rainfall over a 5-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of 1 kilometer of Rancho Grande.]

GENERAL ACCOUNT.

The first glimpse of *Dynastes hercules* at Rancho Grande is recorded in my journal under date of June 6th. I was sitting directly in Portochuelo Pass in full sunshine when an insect attracted my attention by the loud sound of its wings in flight. Usually in flight almost all of the details of an insect are lost, but this beetle hung suspended in midair. Every part of it except the flight wings was

in perfect focus — the pale olive elytra spotted with black, the lower upcurved cephalic horn and the down-curved thoracic horn extending far in advance of the head. I could even see the rich rufous pile, the chestnut fur lining the lower side of the upper horn. The insect flew with a slow steady motion, holding itself almost upright, with the great elytra lifted high out of the way of the flickering flight wings. The general effect was of a diminutive helicopter, the propeller a fuzzy maze, but the whole fusilage clear and distinct. The hercules beetle swung slowly up a few feet, cleared two bushes by only a little and then came roaring past my seat out over the gorge and again back at a higher altitude. I was too surprised, as well as immobilized by reason of a broken leg, to make any effective effort to capture it.

This detail is presented because, with one exception, this was the only time in our two seasons at Rancho Grande when we saw one of these beetles in the daytime. The diurnal discovery in the second instance was only the result of a nocturnal tragedy. On June 22, in Gorge Trail beyond the Pass, I found the head, thorax, fore legs and left elytrum of a female beetle. Within a few feet were bedraggled plumage feathers and much of the wing and a foot of a small screech owl, *Otus choliba crucigerus*, in the gray phase. The killer of the insect had in turn fallen a victim to a tayra whose tracks were about. With the feathers were three more legs of the insect.

On the day following the sight of the hercules beetle in flight, at nine in the evening, a male struck against the glass side of the laboratory, crashing head on. The impact did not even stun the insect and it fell to the sill and there kicked violently about, almost buried in the pile of fluttering moths. This was the first of many individuals which appeared at intervals, both at the laboratory windows and on the white-washed walls on the roof of Rancho Grande, all attracted by the glare of electric lights.

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During the two seasons at Rancho Grande notes were made on sixty-odd beetles, and thirty or forty others were recorded but not collected or studied. Out of the three score insects only five came to the lights on clear nights. The same conditions controlled the attraction as obtained with moths and migratory birds. Heavy overcast, with dense neblina or fog, or nights of actual rain brought the beetles and the maximum of moths to the lights. As in the case of the other organisms, this was probably due to confusion resulting from poor visibility. Several times when I threw a beetle far out into the fog or rain it simply made a wide circle and returned at full speed.

The total count of the sexes amounted to 33 males and 27 females. Six of the former were male minors of extreme type, so that exclusive of these the normal males and females were equal in number. The relative proportions in the two years were quite unlike. In 1945 the males to females were 17 to 6, while in 1946, the proportion was 16 to 21. This may or may not have had something to do with the fact that the latter season was much colder than the former.

As to seasonal abundance, the beetles were rare or absent in the dry season and in April and May, increasing rapidly in June, with both sexes reaching the numerical peak in July, and dropping abruptly in August.

MEASUREMENTS AND WEIGHTS.

If we consider a general lot of males from the point of view of over-all length they resolve into three groups. Nine Majors grade gradually from the extreme of 142 mm., down by gentle intervals of millimeters of 3, 2, 0, 2, 2, 3, 0, 1 and 1. Then comes a group of Mediums with intervals of 10, 7, 10 and 2 mm. Finally extreme Minors show steps of 16, 5 and 6 mm. respectively, the smallest measuring 74 mm. over-all. In the course of two seasons at Rancho Grande six typical Minors were collected, three in June and three in July, and singly, on well separated dates.

When we consider characters in greater detail, the difference between Majors and Mediums on the one hand and Minors on the other becomes much more radical. In the two former the cephalic horn differs chiefly in size, whereas in the Minors it assumes a greatly simplified structure, totally lacking the series of teeth, or with the proximal one represented by a minute nubbin.

The weights of living or freshly killed male *hercules* present the following averages in grams in the three groups; Majors 34, Mediums 23 and Minors 15, the extremes being 37.5 and 15 grams.

Females show no radical distinctions in size. The average is 61.8 mm. in total length, with extremes of 50 and 76 mm., connected

by gradual steps. Their weights average grams, with extremes of 11.5 and 1 grams.

The over-all lengths of Majors and Minors break down into a much more significant comparison of thorax-plus-horn versus body measurements. The average of body length in Majors is 48 mm., in Minors 40 mm. Thorax-plus-horn average 78 in Majors and 40 in Minors. Thus while in normal males the horn element is 137 per cent. of the body, in the Minors it is exactly equal.

Considered in terms of active life habits these measurements acquire considerable significance. At least in the limits of large laboratory cages, where several males and females are confined in a single enclosure the proportional reductions in size in the Minors are a very slight handicap.

As we have seen, the body reduction is very slight, 40 as to 48 mm., whereas the thorax horn is as 40 to 78 mm. Thus the principal loss is in a secondary sexual character, as compared with the vital volant, digestive, respiratory and generative organs of the wings and abdomen. The concomitant functions result in complete failure in combative ability, but no loss in copulative efficiency. In the laboratory I have seen a Minor evade all conflict with other males, fleeing from them at full speed, yet mating successfully with one after another of three females. Whether this advantage would be attained under more natural conditions it is impossible to say. It would most certainly not be the case if jungle mating was preceded by physical contests between rival Major males. Nor can we be sure whether the dwarfing of a few individual males is due to different genetic conditions, or to adventitious deficiency in nutrition during the period of larval development.

The reduction of the thorax with its horn has taken place without radical dislocation of the relative position of the median double tooth. Both in the largest, 142 mm. Major and the smallest 74 mm. Minor, the tooth remains about midway between the posterior thoracic edge and the horn tip. In the Majors this double tooth plays an important part in affording an opposing grip to the corresponding teeth on the cephalic horn. In the Minors it has resolved into two widely separated, wholly useless, blunt, dorsal spikes on the thorax itself.

But the cephalic horn shows distinctive change and variation. The distal dorsal tooth ridge close to the tip is constant in the Majors and Mediums, but, as we have seen, is absent in Minors. The medial teeth vary from none to three, with much variation as to size and position, but with no relation to the size of the insect. The following table shows the relative development of the dorsal teeth of the cephalic horn.

Total Lgth.	Cephalic Horn Dorsal Teeth	
	Proximal	Distal
141	Strong	0
139	Strong	Nubbin
139	Strong	Nubbin
137	Strong	Small
135	3 — joined together	
132	Strong	0
132	Strong	0
131	0	0 (deformed)
130	Strong	Strong
120	Strong	0
113	Strong	Strong
103	Strong	0
101	Nubbin	Nubbin
85	0	0
80	Minute	0
74	Minute	0

COLOR.

The ground color of the elytra appears very characteristic but when compared carefully with the plates in Ridgway it resolves into a variety of colors. Individuals may be light brownish-olive, isabella color, buffy olive, or dresden brown. Less common is a cold buff citrine. I shall lump these in the term brownish-olive for reference to notes in my journal. An unexpected phenomenon was the radical and often rapid change from an almost solid black or blackish-brown to the normal olive, spotted pattern, and back again. The following brief notes are of value only because they refer to the living, newly caught beetles. The numbers refer to those of the sixty specimens on which notes were made.

H2. Brownish-olive sparsely spotted with black.

H6. Minor; Isabella color sparsely spotted.

H7. Jet black. When given banana and feeding, the posterior half of the elytra lightened to buffy olive, black spotted.

H10. Minor; Brownish-black when caught at 11 P.M. At 11:30 began to mate with large female, and at once anterior, lateral area of elytra paled to buffy citrine, spotted with black. 12 midnight, mating. Brownish-olive over whole wing cases, except band down inner margin which is still black. 12:15 A.M., Mating finished. Dark margin has disappeared. This normal pattern remained for six days. Chloroformed and death resulted in a half and half design, the black being present in the form of several broad, irregular lines, extending longitudinally over the buffy citrine ground color. This pattern persisted in preservation.

H8, H9. Both males in buffy olive, black-spotted pattern, one with very small black spots, the other with spots twice as large. H8 changed to solid blackish-brown with two asymmetrical spots of brown on each outer elytrum edge. No change in H9.

H12. Very pale, buffy citrine, with sparse scattering of black spots. No change during

or after several violent battles, but when killed changed to black. The next morning the olive had returned, but with a wholly different pattern of black spots.

H14. Isabella color with five meandering lines of black.

H28. Pale brownish-olive with several, broken, black, longitudinal lines. Two of these reached posterior edge of elytra. One week later the wings turned black in the night, and remained so until four days later when normal pattern returned after death.

H31. Minor. Elytra olive with few black spots. Turned black in three days. After death, assumed a half and half pattern.

H35. Normal coloring with dark, inner, anterior area of wings. Many scattered, very small, black dots.

H38. Upper half, left elytrum black. The rest normal.

H45. Male with deformed cephalic horn. Brownish-olive, heavily lined and streaked, rather than dotted, with black.

H47. Basal fifth of elytra black, with the rest isabella color with a few large black spots.

H48. Pale buffy citrine, streaked with irregular, thin, black lines. A few large black spots at posterior end.

H56. Dresden brown with a few large black spots.

The spots may be solid black, or with a black central dot and an outer black ring, or with a black core and a gradually paling surrounding area. I know of only three males which have remained dark in preservation. One, H43, was sent north alive. In battle, or by accident the dorsal part of the thorax was badly crushed. The dominant color is black with considerable and widely distributed freckling and angular markings of the normal dresden brown.

The greater proportion of the females are blackish mahogany brown, but about forty per cent. show the brownish-olive, black-spotted male pattern to varying degrees. In extreme cases the posterior fourth of the elytra is thus characterized, and the olive extends forward along the outer margin in a wide band, becoming narrower as it approaches the thorax. The olive ground color may be immaculate, or finely or coarsely black-spotted. In one female the right elytrum is conspicuously bi-patterned while the left wing-cover is mahogany.

The color extremes in the male beetles have been known for almost two hundred years. Linnaeus puts *Scarabaeus Hercules* at the very head of the Class of insects, and among his references he includes two from the *Insecten Belustigung* of August Johann Rösel which appeared in 1749. We find two beautifully executed color figures of male *hercules* on different plates. The first is uniformly black, while the second illustra-

tion is brownish-olive with a sparse scattering of small black spots. Both are life-size, about 140 mm. The cephalic horn differs from our Rancho Grande specimens in possessing seven dorsal teeth in place of at most three. But the number and relative development of teeth in both figures show considerable differences.

SENSES.

On the evening of July 30 there were five captive male Majors on the Rancho Grande verandah, all eating banana, and, with their uncleaned cage, giving forth a strong aroma of overripe fruit. The females were all in vivariums in the laboratory. During the evening five additional males came to the dimly lighted cage instead of to the brightly lighted laboratory windows. In this case, it seemed to be the odor of fruit which was dominant over the drawing power of light.

Touching or brushing the thick, furry hair along the ventral surface of the thoracic horn produced no reaction, whereas the least touch of the hind tarsi made the insect jerk suddenly, or start quickly away.

I do not know exactly where, how, or to what extent audibility functions but I am certain that the perception of sounds, or vibrations which produce corresponding effects, does exist. I have mentioned elsewhere the thoracic-abdominal squeaking instrument in *hercules*, which comes into use before encounters and occasionally afterward. A splendid field of investigation awaits the ecological coleopterist who will wring from living tropical beetles auditory methods and reasons, productions and receptions. Examples will offer themselves, from the giant *Dynastes* and *Acrocinus* to tiny coleopters whose frantic neck rubbings upon microscopic instruments indicate sounds, whose faintness or height of pitch prevents excitation of our aural receptors.

It would seem that scent must normally be a definite factor in sexual attraction, and in a small box or cage this is certainly the case. Aside from these limited, abnormal conditions I could find no verification of this theory. Four female *hercules* were placed together in a cage of medium size and exposed on the roof and again in the jungle at the edge of the road some distance from the laboratory. This was done on both clear, overcast and rainy nights. The insects were visited at midnight and in early morning long after the lights in Rancho Grande had been turned off. In no case was a single male found on the cage or in the vicinity.

FOOD.

No opportunity occurred of observing any feeding under natural conditions, but in laboratory terrariums the beetles of both

sexes would feed all day or all night if provided with a succession of bananas, mangoes or other fruit. The insects push head or into the pulp, and slowly work their way softening the fruit as they progress, until it acquires the consistency of mush. Given a hard, green banana, a beetle will eat a deep groove within a few minutes, all the adjacent pulp becoming soft and saturated.

EGGS.

In cleaning out the abdomens of females for preservation, ripe eggs were found first on May 6. The insect was 76 mm. in total length, the record for this sex, and the eggs were 31 in number, also a record. The eggs which were about to be laid, were equal-ended, broad ovals, 3.5 by 4.3 mm. The shells were white and as hard as those of a bird or lizard. Under high power the surface was seen to be covered in rough lines by a multitude of short, thin ridges, each minutely toothed along the summit. The contents were a homogeneous, thick, white liquid.

This was the only occurrence of ripe eggs before mid-June. From this date the individuals rose gradually to a climax of breeding in mid-July with a single instance in mid-August. The ripe eggs were sharply set off from a multitude of very small, undeveloped ova. The occurrences were as follows, in order of number: 5, 8, 9, 14, 15, 16, 20, 21, 25 and 31 eggs. There was no relation between number of eggs and either size of the female or date of ripeness.

JOURNAL NOTES ON COMBAT BEHAVIOR.

(The present account possesses an especial interest in satisfactorily demonstrating the adaptive significance of male cephalic and thoracic horns in *Dynastes hercules*. Taken in connection with an earlier paper on *Megasoma elephas* and *Strategus aloeus*,² proof is presented that, at least in three cases of neotropical species, secondary sexual characters are of definite use in specialized combats between male beetles.

(It seems hardly necessary to mention the intentional use of anthropomorphic terms such as "accepting a challenge" or "combats with a rival." If we attempt to go purist in an account like this, we must invent a wholly new set of terms for a coleopteran glossary, which is manifestly silly. We have armed beetles fighting with one another over the possession of a desired female. The combatants make full use of specially adapted weapons. As long as we accept the mental activations of the whole performance as analogous, and only the visually apparent mental end results as homologous (as between vertebrate *vs.* invertebrate), I see no need for dictional apologia. Even "as ifs"

² Beebe, *Zoologica*, 1944, Vol. 29, No. 8, pp. 53-58.

may be understood, and therefore omitted).

July 9: Put a large Major (H2, 142 mm.) and a small Minor (H6, 80 mm.) together and they fought at once. After several casual feints the large beetle, suddenly aroused, seized the small one in a scissors grip of the two horns, and started away with him. After going about a yard, the Major tripped, fell and both rolled over. The Minor pushed himself up on his feet and rushed off, leaving his giant rival kicking helplessly on his back. This was the first exhibition of actual carrying or transportation. The Major had no difficulty in holding the small beetle well aloft, and in walking slowly off, carrying a weight one-half that of his own.

The next day the same Major and Minor were put in with three females. Both mated at once, but the Major soon left his female and attacked the other mating pair. In spite of his utmost efforts, he could not dislodge the Minor although both he and his female were rolled over and over. The unfortunate female bore much of the brunt of the attack. The Major could not open his forceps sufficiently to enclose and lift the mated pair. He soon gave up and returned to his female.

July 16: A new-caught Minor showed more vitality and activity than has any Major. Placed with five Majors and four females the small male mated with all the females in turn, and several times in succession with two of them, while the much larger beetles took time off from feeding to mate with only one or two. After careful observation, I believe that the copulations of the Minor were as complete and successful as those of the Majors.

In three combats with the two Majors the Minor showed no lack of courage and rushed his giant opponents, but always to no purpose. He was invariably seized and carried off the field high in air, in the massive, toothed horns. The Minor always attempted the conventional pincer grip of his species, in spite of the fact that the small size of his fighting weapons made them wholly inefficient and ineffective.

July 22: A very large Major came this evening to a cageful of four others eating bananas in the open verandah of Rancho Grande. I put the newcomer with the others, and he instantly crawled to a bit of fruit and attacked another male already deep in the pulp. The feeder was seized, carried about and ultimately banged down on the concrete floor. This stirred up another pair of beetles which clinched at once, and were in turn assaulted by the new-caught beetle. He secured a good grip on the preoccupied fighters and lifted both into the air, staggered about eighteen inches and dropped them heavily. This time he successfully lifted and transported twice his own weight. Immediately all three ceased fighting and

devoted themselves to the same half of a banana.

July 30: Day after day for a week I have matched two Majors against each other. One is dominantly Black and the other Olive. Black measures five inches over-all and weighs twenty-six grams; Olive is four and three-quarters inches and twenty-four grams. The equality is thus almost perfect, and I never saw that the slight discrepancy conferred or denied any advantage. Although the color distinction was a satisfactory method of telling them apart at a distance, yet even it was not permanent and Black might in time become Olive, and vice versa.

In the days intervening between combats I varied the situation, society and occupation of the two beetles. Black might be caged alone while Olive was given the association of several females; Olive might be furnished with an unending feast of banana, while Black fasted. Olive might be annoyed by the continual but futile attacks of a pair of bulldog-like Minors, while Black was kept in darkness and quiet for sleep or what corresponds to scarabaeian meditation. Yet in one conflict after another, day after day, neither surfeit of food, sex, annoying combats or restful quiet altered, in any way, the respective method of attack, or changed the very distinct personalities shown in contests between the two heavy-weight hercules beetles.

The general herculean battle routine proceeded as I have described it elsewhere, but the distinctive, individualistic sequence is as follows: The Black rushes the contest. Throughout what we might call Rounds, he seizes the other, raises him on high and stumbles about with him, and finally bangs him down. During all this Olive is perfectly quiescent, putting up just enough defence to show he is not actively trying to escape. His very relaxation seems to preserve him from injury, as is so often the case in human contests or other activities. When slammed down for the fourth or fifth time, the lethargic Olive is suddenly obsessed by what appears to be a most unbee-like rage, and from now on the melee is full of reciprocal action. The little bulging eyes must see more than they appear to, for again and again I have seen Olive avoid the scissors grip and snap of his dark opponent, and with what I can call nothing but skill, suddenly turn upon Black, grip him, shift his hold and rising so high that he seems on the point of overbalancing backwards, hurl the bigger beetle, with his handicap of two grams, once or as many as three times. Whereupon the erstwhile victor turns and scuttles off as fast as his six legs will carry him.

Seven times in the course of nine days this same performance took place with iden-

tical action and counter action. Only with respect to the last phase did variety enter in. Always Olive was at first the under dog; invariably at the end he was victor. But twice he fled as I have written above; once he lifted his great citrine shards and unlimbered the wide expanse of transparent, amber flight wings, and only a quick grasp on my part kept him from helicoptering off the field of battle, over the jungle, into the sky. Two other times Olive watched his vanquished rival vainly kick as he swivelled around on his back, and both of these times made his way to the nearest female and mated. The two remaining times his rage failed to cool and he continued the battle until Black was reduced to complete immobility, although ultimately he fully recovered. On these occasions Olive wandered away to a split banana, thereupon subordinating all other emotions.

GENERAL COMBAT BEHAVIOR.

Encounters between male hercules beetles are usually rather brief, and are dependent on the willingness of each to fight. One may be feeding or resting quietly when a second male approaches. Before any actual contact, when still several inches apart, the beetle which is eager for the engagement moves the thorax up and down, producing a rhythmic series of zizzing squeaks. There is not the slightest doubt that this is heard and understood. Even if mouth and head are buried deep in mushy banana plup, the eater gives a jerk on hearing the sound, and assumes for a moment what may well be an audient immobility. He may keep on guzzling or may back away practically into the waiting grip of the squeaker.

If the feeder chooses to accept the challenge this is evident in a complete change of demeanor. Ordinarily these hercules beetles move and feed and react in the same slow, bungling way common to most of their family. The deliberate awkwardness of June bugs and cockchafers is theirs. But at the sound of the hissing, or actual contact with another male who intends combat, there occurs a radical change. Movement shifts to quick, nervous jerking, evident whether the insect is standing still or walking. When combat is refused, the beetle turns and retreats rapidly, the gait soon shifting to the usual slow, aimless progress.

If the pacifist is picked up in the hand and brought close to the still squeaking male, the sudden revitalization can be distinctly felt in the held insect. The legs jerk spasmodically in mid-air and the beetle may, in turn, begin squeaking on its own behalf. If the two are brought into contact and irritated, a fight will usually ensue. The hissing squeak may now cease and another phase of the routine take its place. This is

a rapid jiggling up and down of the anterior part of the insect, an extension and flexion of the fore legs, recalling the corresponding exhibition of *Anolis* and other lizards. More frequently this diminutive war-dance is performed by the winner, after the termination of the fight.

The sequence of the actual encounter is unvarying. The two meet head on, but there is much less rearing and absolutely none of the attempts at tripping so characteristic of *Megasoma elephas*.³ The projecting horns touch and click, spread wide and close, the whole object of this opening phase being to get a grip outside the opponent's horns. When the four horns are closed together there is a dead-lock. All force is now given over to pinching, with the apparent desire to crush and injure some part of head or thorax. When the beetles are quiet in this attitude for a few seconds, nice details in adaptive arrangements for protection become evident. One such is the oblique chitinous bar stretching part way across each eye, exactly like a skeleton visor, or the nose-guard on the helmet of an eleventh century medieval knight.

Again and again, both opponents back away, freeing their weapons, and then rush in for a fresh grip. When a favorable hold is secured outside the other's horns, a new effort, exercised with all possible force, is initiated. This is a series of lateral jerks either to right or left, with intent to shift the pincer grip farther along the thorax as far as the abdomen and if possible on to mid-elytra. In addition, if the hold is at first confined to the incurving horn tips, the shift must be ahead, so that the final grasp brings into play the two opposing sets of teeth on the horns. Once this hold is attained and a firm grip secured the beetle rears up and up to an unbelievably vertical stance. At the zenith of this pose it rests upon the tip of the abdomen and the tarsi of the hind legs, the remaining four legs outstretched in mid-air, and the opponent held sideways, kicking impotently. This posture is sustained for from two to as many as eight seconds, when the victim is either slammed down, or is carried away in some indefinite direction to some indeterminate distance, at the end of which the banging to earth will take place. After this climax, if the fallen beetle is neither injured nor helpless on its back, it may either renew the battle, or more usually make its escape.

The general sequence of combat is almost unvarying, but the certainty of outcome is another matter. For example, the successful impersonator of the part of his namesake Hercules, may by chance happen to trip over a twig or his own feet, while carrying the Antaeus actor high in air. Both then may

³ Beebe, 1944, *Zoologica*, Vol. 29, No. 8, pp. 53-58.

roll over and over, whereupon, if the erstwhile Antaeus is the first to rise, he may reverse his mythological part, assume in turn the herculean role and start off with his struggling burden on the path to victory. His course may take him over the identical ground which he had just traversed in the jaws of the other male.

Or again, after such an accident, both beetles may scramble to their feet, rush off in opposite directions, and if their path should cross a banana, all subsequent concern with combat may be lost in gustatorial delights.

There is no doubt of the crushing power of the two opposed horns, but I have never been able to feel it exerted on my fingers. The toothed elements of the Majors and the sharp tips of the horns of the Minors can press hard enough on flesh to be painful, but the insects seem to recognize a tissue foreign to that of their own kind, and never exert full force. I have caused a quick shift to a severe crunch by suddenly substituting the elytra of a beetle for my fingers, when the hard, resistant shards bend beneath the increased pressure.

With our ear held close to the fighters we can distinctly hear the clash of chitin on chitin, changing to a scraping as the grip shifts sideways. When the teeth come into play, a third sound, a real crunch, is audible, as the wing covers bend or even break.

The combats between a full-sized Major and a Minor were always a foregone conclusion. The small one never refused a tilt and would rush pellmell into the encounter, squeaking as loudly as the giant. But it was no use. His instincts remained unchanged and his undersized dwarfed weapons which could not encompass a beetle of his own size, were useless against the girth and weight of the Major. His opponent simply clinched his long horns around the smaller beetle and carted him away high in air. His very lightness seemed to be an advantage in the end, for only once did I see a Minor injured or stunned by the slamming to the ground.

TRANSPORTATION OF THE FEMALE.

Observations on female beetles being carried about between the horns of the males are few, scattered and lack details. None, so far as I know, have been checked or reconfirmed. Bateson and Brindley (*P.Z.S.*, 1892, p. 590) quote Baron von Hugel indirectly: When these Javan beetles, *Xylotrupes gideon*, were untied, "the males immediately sought out the females, and seizing them transversely, carried them about, held between the two horns, with evident satisfaction. He tells us that this was observed again and again, and was clearly a definite habit. The males with small horns, though unable to lift the females, nevertheless made ludicrous

efforts to do so." The same habit was observed in a pair of *Chalcosoma atlas*.

In *Country Life* for August 28, 1942, M. Forster Knight, writing of stag beetles, presumably *Lucanus cervus*, says that the male occasionally lifted his mate and carried her for some distance. The battles of the males are described as "lift, carry and toss."

Until our experience with hercules beetles at Rancho Grande I had never believed the story of the male carrying off the female, held firmly between its horns. One day after a Major had speedily defeated and transported a small Minor, and flung it down according to schedule, the Major came upon a female and with no hesitation picked her up and walked off. She was held rather awkwardly and soon one of her dangling legs tripped him and she was dropped. I considered this a blind, instinctive continuation of the transportation of the Minor.

On subsequent occasions, however, this performance was repeated and with such deliberateness that I was compelled to admit it as an accepted fact. The cause remained insoluble, and the certainty of occurrence could not be foretold. Time after time a male would approach a female, whether she was feeding or moving about, and mate at once. On other occasions he would touch her, playing over her back with his antennae, and soon pick her up and walk away. Twice females were carried as far as I dared let them go into the underbrush. At other times the female was dropped gently (not slammed down as would be the case with another male) and left while the Major went to a banana and fed. Other carryings were indeterminate because of the confined space in a laboratory cage. Once only did I see a mating follow a short transportation. What significance this has in the sexual economy of hercules when the event takes place normally at night in the jungle, I cannot even guess. Miss Crane obtained good color movies both of all phases of combat and of the female being picked up, raised high and carried out of the picture.

DISCUSSION.

In *hercules* there seems to be a complete absence of any courtship or display by the male in respect to the female. The relationship of the sexes is confined to direct mating in which the female is receptively passive. There is also an occasional, inexplicable, aimless transportation of the female a short distance.

The males use their horns in combat, utilizing the specialized shape and position of these characters in a specific routine. This instinct and method persists in Minors whose horns are too small and abortive to be effective. Squeaking and repeated bowing are also indulged in before and after the encounters.

SUMMARY.

Dynastes hercules is a very large scarabid, the males armed with specialized horns of great size. This species is not rare at Rancho Grande, coming to lights on overcast or rainy nights. Notes are presented on abundance, proportion of sexes, size and weight, Major and Minor males, change of pattern and color, food and eggs.

Especial attention is given to combat behavior, the handicap of the Minor males, the individuality of combat routine, the unexplained transportation of the female, and comparison with the very different method of combat of *Megasoma elephas*.

EXPLANATION OF THE PLATES.

PLATE I.

- Fig. 1. Male Minor, female and male Major (preserved specimens).
 Fig. 2. Living hercules beetle, showing size.
 Fig. 3. Beginning of combat of two Major males, showing extremes of pattern and color.

PLATE II.

- Fig. 4. Major male with a Minor male held between its horns.
 Fig. 5. In combat between two Major males one is lifted partly off the ground.

PLATE III.

- Fig. 6. The beetle is lifted clear off its legs.
 Fig. 7. The beetle is raised twice its own height into the air.

PLATE IV.

- Fig. 8. The victor is supported by only four legs.
 Fig. 9. The victor is now almost vertical supported by only the two hind legs and the tip of the abdomen, preparatory for the downward smash.
 Fig. 10. Victorious male approaching female.
 Fig. 11. Male obtains a grip on the thorax of the female.
 Fig. 12. Male carrying off the female.

Figures 8 to 12 inclusive are enlarged from 16 mm. kodachrome motion picture film. All illustrations of living beetles by Jocelyn Cran-



FIG. 1.



FIG. 2.

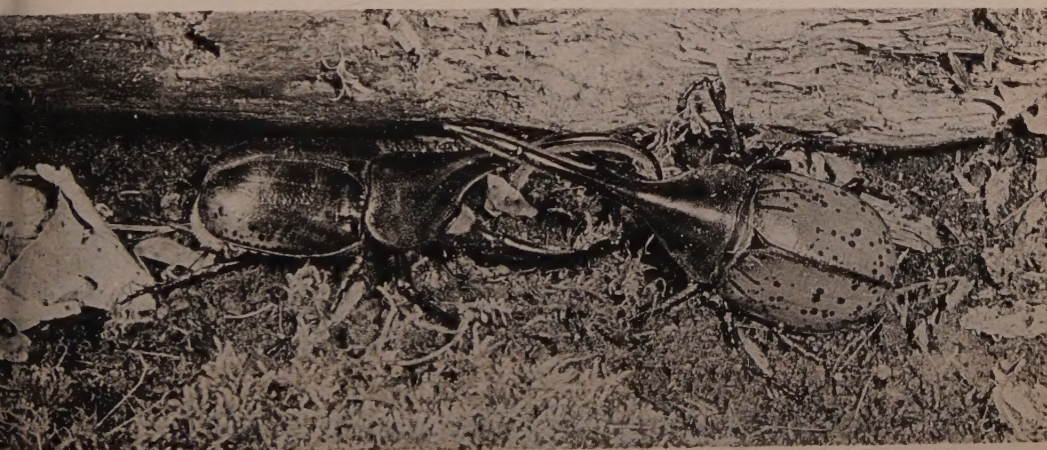


FIG. 3.

NOTES ON THE HERCULES BEETLE, *DYNASTES HERCULES* (LINN.), AT RANCHO GRANDE, VENEZUELA, WITH SPECIAL REFERENCE TO COMBAT BEHAVIOR.



FIG. 4.



FIG. 5.

NOTES ON THE HERCULES BEETLE, *DYNASTES HERCULES* (LINN.), AT RANCHO GRANDE, VENEZUELA, WITH SPECIAL REFERENCE TO COMBAT BEHAVIOR.



FIG. 6.



FIG. 7.

NOTES ON THE HERCULES BEETLE, *DYNASTES HERCULES* (LINN.), AT RANCHO GRANDE, VENEZUELA, WITH SPECIAL REFERENCE TO COMBAT BEHAVIOR.



FIG. 8.



FIG. 9.



FIG. 10.



FIG. 11.



FIG. 12.

NOTES ON THE HERCULES BEETLE, *DYNASTES HERCULES* (LINN.), AT RANCHO GRANDE, VENEZUELA, WITH SPECIAL REFERENCE TO COMBAT BEHAVIOR.